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# The Transformation of Energy by *Lucifer chacei* (Crustacea, Decapoda)[1]

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ABSTRACT: A laboratory study of energy transformations by the pelagic decapod crustacean *Lucifer chacei* was made. Three combined stages were cultured and studied: the protozoea-zoea stages, the combined early and late schizopod stages, and the combined adult stages. Growth rates, dry weight, ash content, and calorific values were determined for each. Number of calories per hour ingested, assimilated, and respired were also determined for each of the combined stages. An energy flow diagram was constructed from the data.

Growth from egg to adult took slightly more than 3 weeks. Protozoea-zoea and schizopod stages assimilated 10.1 percent and 10.4 percent of ingested *Dunaliella tertiolecta*. Adults assimilated 7.7 percent of ingested *Dunaliella tertiolecta* and approximately 22 percent of ingested *Artemia salina* nauplii. The data indicate that a change from herbivorous larvae to omnivorous adults may have to occur in the natural environment because the older stages cannot obtain enough energy for growth from phytoplankton alone. When data for all stages were combined, gross growth efficiency and net growth efficiency for *Lucifer* were approximately 10 percent and 81 percent, respectively.

The flow of food energy, measured as calories, through populations provides a quantitative basis for studying the dynamics of a community or ecosystem. The flow of energy through a single-species population can be used to determine the role of that species within its community or ecosystem. To determine energy flow through an aquatic population, one must first measure the quantity of energy ingested. For zooplankton this energy may be in the form of living phytoplankton or other zooplankton, although nonliving dissolved and particulate food sources may also be important (Baylor and Sutcliffe 1963, Conover 1964). Food energy takes numerous pathways as it passes through an animal. Part of the material is assimilated, and part passes out as feces. The ratio between calories ingested and calories assimilated is known as the assimilation efficiency (Conover 1964, Kozlovsky 1968). In this paper assimilation efficiency will just be called assimilation.

The assimilated energy is used in different ways. Some is used in metabolism and can be measured as respiration. Some is incorporated into reproductive products and, in Crustacea, into the exoskeletons (Lasker 1966); this energy is lost eventually. The rest of the assimilated material is incorporated into body tissues.

My study was concerned with laboratory measurements of the rate of flow of energy through a population of *Lucifer chacei* (Borradaile) Bowman from Kaneohe Bay, Oahu, Hawaii. The work included a study of the transformation of energy by two combined groups of larval stages and the adults.

*Lucifer chacei* is a pelagic sergisted shrimp that appears to have a wide distribution in the tropical and subtropical Pacific. Edmondson (1923) and Hiatt (1947) reported it (as *Lucifer faxoni* Borradaile) from the North Central Pacific, and Chace (1955) noted its occurrence in the Marshall Islands. Until recently (Bowman 1967), this species was considered to be identical with *Lucifer faxoni* Borradaile, which has a wide distribution in the Atlantic (Hiatt 1947). Despite this wide distribution, little work, except systematics, has been done on this genus. Brooks (1882) studied the morphology and develop-

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ment of the genus *Lucifer*, and Woodmansee (1966) observed some aspects of its vertical migrations. Piyakarnchana (1965) has shown that *Lucifer chacei* is an abundant member of the plankton in Kaneohe Bay, Oahu. Its role in this pelagic community, except for its being a significant item in the diet of the adult Hawaiian anchovy *Stolephorus purpureus*, is unknown (Hiatt 1951).

The following aspects of energy transformation by *Lucifer chacei* are considered in this study: grazing rates by young and adults on phytoplankton, predation by adults on *Artemia salina* nauplii, and assimilation of this material as estimated by using the radionuclide $^{35}S$. Calories per ash-free gram, respiration rates, growth rates, and occurrence of molts in young and adults are also estimated. An overall energy budget has been calculated from these data.

## MATERIALS AND METHODS

### *Food Organisms*

Four different phytoplankters were used as food. Two of the species, *Phaeodactylum tricornutum* and *Cyclotella nana*, are diatoms; and the other two, *Dunaliella tertiolecta* and an unidentified form, are green flagellates. Although *Lucifer* appeared to do well on the diatoms, the flagellates were easier to count and were used for most experimental work.

The unidentified flagellate culture was started from a whole water sample collected in the lagoon at Coconut Island, Oahu. *Cyclotella nana* and *Dunaliella tertiolecta* were grown in medium "f/2" modified from Guillard and Ryther (1962). *Phaeodactylum tricornutum* and the unidentified flagellate were grown in a second medium modified from Loosanoff and Davis (1963). "Combistrep," a liquid bacteria inhibitor, was added (0.19 ml/liter) to both media to reduce bacterial growth. The algae were maintained at approximately 25° C in 2.8-liter Erlenmeyer culture flasks filled with filtered, enriched seawater.

The recently hatched nauplii of *Artemia salina* were also used for food for adult *Lucifer chacei*. Anraku and Omori (1963) and Lasker (1966) have indicated that this is a suitable food for carnivorous or omnivorous zooplankton.

### *Lucifer chacei*

Initially, all stages of *Lucifer chacei* were collected by towing 1-m or 0.5-m diameter conical plankton nets, of mesh size 0.33 mm, near the surface of Kaneohe Bay where the shrimp are very abundant. In the latter part of this study all stages were collected with a dip net under a night light suspended above a dock at the Coconut Island Laboratory. Animals collected in this manner were injured less frequently than those taken in conventional tow nets, and few other organisms the size of adult *Lucifer* were attracted.

To determine energy use by *Lucifer* throughout its life history, I studied the animals from egg to adult stages. Larvae were obtained by placing gravid females in approximately 1,500 ml of filtered seawater. The eggs hatched in 2 days or less. Small amounts of phytoplankton were added as food. Soon after the larvae were released, the females were removed, and some of the larvae were placed individually or in small groups in 300 ml of water. The water was changed infrequently or not at all during the first 7–10 days of growth. Cultures were kept on a slowly oscillating shaker table and phytoplankton were occasionally added to maintain a high density of cells. Measurements of size were made at 2-day intervals.

### *Measurements of Length, Weight, Percent Ash, and Calories*

The length of *Lucifer* usually was measured in all stages as the distance between the most anterior curvature of the eye and the last abdominal joint; an ocular micrometer was used for the measurements. Measurements were made after the water was removed and each animal had been straightened. Dry weights of phytoplankton were determined by filtering single-species cultures through a dried Millipore filter (0.45 $\mu$) of known weight and drying the filter and collected algae after rinsing them with distilled water. The amount of weight lost due to rinsing a blank filter was also determined. Number of cells per milliliter was determined before filtering, and this number multiplied by the volume (ml) of filtered culture gave the total number of cells.

Dry weights of animals were determined by first rinsing the animals briefly with distilled water and then by placing a known number in a desiccator in a constant-temperature oven at 60° C (Lovegrove 1966). A large number (80–550 per sample) of the zoea and schizopod stages were dried to obtain accurate weights. Weighings were made with either a Mettler semimicrobalance or a Cahn gram electrobalance. The Cahn balance was always used for weighing small quantities of materials.

Ash determinations were made by placing dry, weighed animals in a Thermolyn constant-temperature furnace at 450°–500° C until constant weight was reached (Paine 1964). Calorific values of larval stages of *Lucifer* were determined with a Phillipson Oxygen Microbomb Calorimeter.

*Feeding Experiments*

To determine grazing rates on phytoplankton, I placed *Lucifer* in filtered seawater in flasks of various sizes. Adults were placed in 100 or 200 ml of water in 300-ml flasks; schizopod stages and combined protozoea-zoea stages were placed in approximately 30 ml of filtered seawater in 100-ml flasks. *Dunaliella* or the unidentified flagellate was then added to give a suspension of greater than 15,000 cells/ml. Cells were counted with a model "B" Coulter Counter. An aperture tube with a 100-$\mu$ orifice was used throughout this study. The small flagellate, which was approximately 3.7 $\mu$ in diameter, proved difficult to measure precisely with the 100-$\mu$ orifice. Therefore, *Dunaliella tertiolecta*, approximately 12 $\mu$ in diameter, was usually used. All phytoplankton grazing experiments were carried out in complete darkness.

All solutions were well stirred before a count was made. Periods of feeding lasted from 8–16 hours, and grazing rates were calculated from the difference between the number of algal cells in the flasks per unit time after corrections had been made for population changes in control flasks. Volumes swept clear (Gauld 1951) and the instantaneous rate of decrease in the phytoplankton population caused by grazing were determined.

Data concerning ingestion of *Artemia* nauplii were obtained by two different methods. The first method was used to determine predation rate by individual *Lucifer* on *Artemia*. Single adult *Lucifer* were placed in 500-ml glass jars containing 300 ml of filtered water, and a known number of *Artemia* nauplii were added. A few hours later the *Lucifer* were removed and the water was refiltered to determine the number of nauplii remaining. The second method was used to determine average predation rate. Seven to 12 *Lucifer* were placed in each of several 8-inch-diameter culture dishes filled with 1,400 ml of filtered water, and a known number of *Artemia* nauplii (usually about 150) was added. After a few hours, the *Lucifer* were removed and the water was filtered to determine the number of remaining nauplii. Experiments were carried out either in daylight or darkness.

*Respiration*

Respiration was measured by a "micro-Winkler" technique. Seven to 12 adults, or up to 125 of the younger stages, were placed in filtered seawater in 10-ml stoppered Erlenmeyer flasks for 2–4 hours. Only healthy animals were selected for these experiments (as determined by swimming activity), and animals that did not survive were not counted in the calculations. Activity in the flasks was observed to be similar to activity in large aquaria and feeding chambers. All measurements were made in a constant temperature laboratory at approximately 25° C. Experiments were carried out during all periods of the day in daylight and darkness. Respiration was calculated from the difference between control flasks without animals and those containing animals.

*Assimilation*

The isotope $^{35}S$ was used to determine assimilation. This isotope was chosen because it has a relatively long half-life (88 days) and a long residence time in the tissues of Crustacea (Sidney J. Townsley, personal communication).

A first experiment was designed to determine assimilation of animal material by adult *Lucifer*. Two-hundred-fifty ml of *Phaeodactylum* were cultured for 24 hours in a solution containing 900 $\mu$Ci $^{35}S$. The algae were then fed to recently

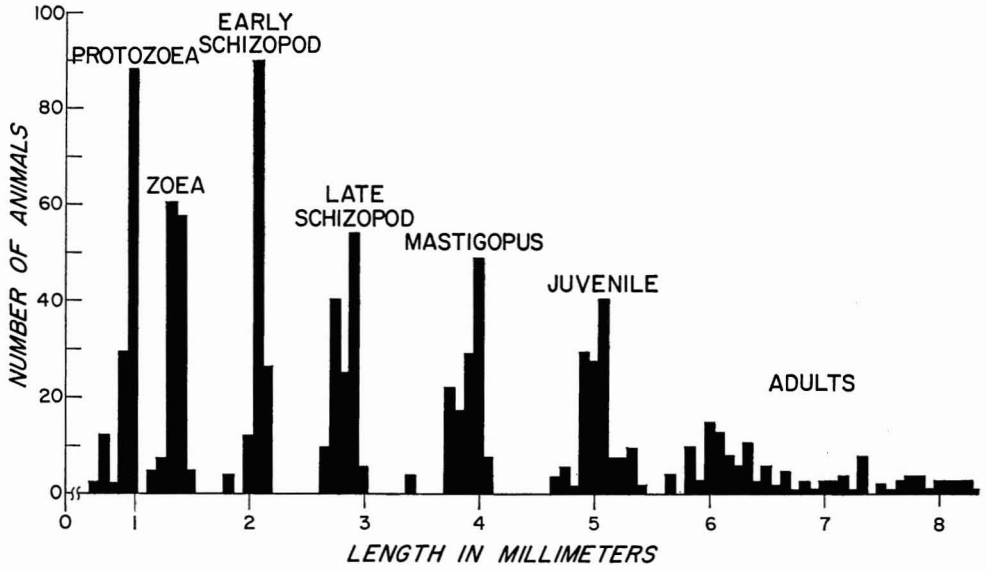


FIG. 1. Size distribution of all major morphological stages of *Lucifer chacei* except nauplius. All values corrected to 135 animals per stage.

hatched *Artemia* nauplii. The nauplii were allowed to feed for 10 hours, then were rinsed and placed in filtered seawater for 18 hours to allow the guts to clear. Groups of 14–35 radioactive *Artemia* were placed on Millipore filter pads in order to establish the number of disintegrations per *Artemia*. Between 24 and 46 then were fed to each *Lucifer*. Feeding continued for 6–7 hours in one set of experiments and 12–13 hours in a second set. The *Lucifer* were then removed and placed in filtered water for 15 hours to clear their guts of unassimilated materials. Each sample was placed in a Nuclear Chicago gas flow radiation counter until 2,000 disintegrations had been recorded.

Assimilation of phytoplankton by three combined stages of *Lucifer* was also determined. A 500-ml *Dunaliella* culture was cultured with 900 $\mu$Ci $^{35}S$ and allowed to grow for 24 hours. The number of cells per ml was determined with the Coulter Counter, and aliquots of this solution were filtered, rinsed, and collected on Millipore-filter pads for determining the disintegration rates of the *Dunaliella* cells.

Several combined schizopods (30–45) or combined protozoea-zoea (62–81) larvae were placed in 100-ml beakers containing 10 ml of the radioactive *Dunaliella* culture and 25 ml of filtered water. Adults were placed in 100 ml of filtered water, and 20 ml of radioactive *Dunaliella* suspension were added. Controls to determine changes in phytoplankton populations not due to grazing were prepared in the same manner but no animals were added. Uptake from solution was determined by placing *Lucifer* in a radioactive solution without phytoplankton.

The number of cells ingested was determined with the Coulter Counter. All animals were allowed to feed for approximately 12 hours and then were rinsed and placed in filtered seawater for 15 hours to clear their guts. The algae and shrimp then were dried and "counted" until 20,000 disintegrations had been recorded in each sample. Assimilation was taken as the ratio between the radioactivity of food ingested and the radioactivity of the animals with cleared guts.

## RESULTS

*Lucifer chacei* proved to be a hardy laboratory animal. It responded well to a variety of food types, container sizes, and occasional rough handling.

As the study progressed *Dunaliella tertiolecta* proved to be the easiest food to culture and

TABLE 1

GROWTH OF *Lucifer chacei* FROM EGGS HATCHED IN THE LABORATORY

| ITEM | DAYS AFTER HATCHING | | | | | | |
|---|---|---|---|---|---|---|---|
| | 6 | 10 | 13 | 15 | 17 | 19 | 23 |
| Eggs Hatched on 26 March 1968 | | | | | | | |
| Mean Size | 2.4 | 4.1 | 4.7 | – | – | – | – |
| Standard Error | 0.20 | 0.23 | 0.17 | – | – | – | – |
| Number of Measurements | 5 | 5 | 5 | – | – | – | – |
| Eggs Hatched on 19 August 1968 | | | | | | | |
| Mean Size | – | 4.0 | 4.9 | 5.7 | 6.8 | 7.5 | 8.1 |
| Standard Error | – | 0.11 | 0.16 | 0.17 | 0.20 | 0.23 | 0.13 |
| Number of Measurements | – | 15 | 9 | 13 | 14 | 11 | 8 |

TABLE 2

WEIGHT AND ENERGY CONTENT OF STAGES OF *Lucifer chacei*

| ITEM | ADULT | SCHIZOPOD | PROTOZOEA-ZOEA |
|---|---|---|---|
| Mean Size (mm) | 8.0 | 2.4 | 1.1 |
| Wet Weight (mg) | 0.96 | – | – |
| Number | 1 | – | – |
| Dry Weight (mg) | 0.161 | 0.0173 | 0.0167 |
| Number | 3 | 3 | 3 |
| Standard Error | 0.0023 | 0.0006 | 0.0001 |
| Percent Ash of Dry Weight | 16.25 | 34.56 | 47.50 |
| Number | 4 | 3 | 3 |
| Standard Error | 0.24 | 1.37 | 0.54 |
| Calories/g Dry Weight | 4,818 | 4,282 | 4,117 |
| Number | 3 | 3 | 3 |
| Standard Error | 8.59 | 30.67 | 35.84 |
| Calories/g Ash-Free Dry Weight | 5,770 | 6,570 | 7,900 |
| Calories/Animal | 0.776 | 0.0741 | 0.0688 |

count using the Coulter Counter 100-$\mu$ orifice. This species also tended to clump and sink less than the diatom species. For these reasons it was used as the principle food throughout most of this study.

All of the general developmental stages of *Lucifer chacei* described by Brooks (1882) were observed, but the nauplius stage was not considered here because it exists for only a few hours. The size frequency distribution of 477 individuals of all stages collected live from Kaneohe Bay is shown in Fig. 1. At least 55 individuals in each stage except the early schizopod were measured. Comparison was facilitated by adjusting all values to 135 animals per stage, which was the number of adults measured. Animals raised in the laboratory were comparable in size at the various stages to net-collected animals. Fig. 1 indicates that discrete gaps in length generally occur between certain larval stages of *L. chacei*. These correspond to the major morphological changes observed by Brooks (1882).

Growth rates of animals reared in the laboratory can be computed from age and mean size data in Table 1. Usually growth from eggs to adults (7–8 mm) takes approximately 20 days in high food concentrations. Qualitative observations of the growth of several hundred other individuals fed on a variety of foods indicated that growth from larvae to adult proceeds at about the same rate. Growth to the mean size used in calorific determinations (8.0 mm) was estimated to take 23 days. Data on weight, ash content, and calorific value of the three combined stages of *Lucifer* are presented in Table 2.

TABLE 3

FEEDING RATES OF ADULT *Lucifer chacei* ON TWO TYPES OF PHYTOPLANKTON

| ANIMAL | NUMBER | FEEDING RATE (CELLS/h PER ANIMAL) MEAN | STANDARD ERROR |
|---|---|---|---|
| *A.* Small Flagellate | | | |
| Adults—Starved | 4 | 82,500 | 2,200 |
| Adults—Fed or Fresh | 6 | 44,000 | 2,400 |
| *B. Dunaliella tertiolecta* | | | |
| Adults | 5 | 4,850 | 640 |
| Schizopods | 3 | 2,340 | 430 |
| Protozoea-Zoea | 4 | 805 | 100 |

The mean dry weight of the combined protozoea-zoea stages is about the same as that of the combined schizopod stages. However, the ash content of the protozoea-zoea stages is greater than that of the schizopod stages of *Lucifer*.

Recently captured or previously fed adult *Lucifer*, when placed in 300 ml of a medium containing approximately 150,000 small flagellate cells/ml, filtered a mean of 44,000 cells/h per animal (Table 3*A*). Starved animals (not fed for at least 24 hours) filtered at a higher rate, and hence were not used in further work. Filtration of such small organisms may have been accomplished by setae on the mouthparts. Constant movement of the swimming legs was observed and may have helped create water currents toward the mouthparts.

During the experimental period, the small flagellate culture became contaminated with a dinoflagellate, after which *Lucifer* did not appear to ingest many cells from the culture. Because of this contamination and problems involved in counting such small organisms, the rest of the feeding experiments were done with *Dunaliella*. Table 3*B* shows the results of several experiments on feeding *Dunaliella* to different stages of *Lucifer*.

All stages of *Lucifer* beyond the late schizopod captured and assimilated *Artemia salina* nauplii. Presumably they feed on other zooplankton in Kaneohe Bay, but mastication is so complete that stomach analysis of specimens from Kaneohe Bay did not yield any identifiable remains. Crab zoea were not eaten in the laboratory.

*Lucifer* often appeared to be passive when capturing *Artemia*. Feeding was initiated by a nauplius swimming close to the ventral anterior area of a *Lucifer*, although occasionally adults were observed to lunge a few millimeters to catch a nauplius. The prey were held outside the body and masticated for about 15 minutes. One juvenile only 5 mm long was able to capture a nauplius 0.42 mm long.

Although rates of predation on *Artemia* often were very different among individual *Lucifer* over short time periods, the mean rates between long-term experiments were very similar (Table 4) for animals fed individually in bottles containing 300 ml of water. Between 1.7 and 1.8 *Artemia* were ingested per h/animal. This rate corresponds to an average of approximately 260 nauplii ingested per milligram *Lucifer* dry wt per day, a higher value than reported for larger pelagic Crustacea (Lasker 1966).

The ingestion rate was much lower for groups of *Lucifer* fed in 8-inch culture dishes containing 1,400 ml of water (Table 5). Approximately the same numbers of *Artemia* per volume of water were used as in the previous experiments, but the volume of water per *Lucifer* was approximately one-half. A second series of experiments in the 8-inch culture dishes (Table 5) indicated that *Lucifer* ingested more *Artemia* when algae were present than when they were absent. Rates in individual bowls rose when phytoplankton was added but remained about the same when it was not (Table 5*B*). Predation rate of *Lucifer* feeding on *Artemia* apparently was not affected by time of day or by light (Table 4).

The calorific value of brine shrimp nauplii was estimated to be 0.0114 calories per individual, based on Slobodkin's and Richman's

TABLE 4

FEEDING RATES OF INDIVIDUAL ADULT *Lucifer chacei* ON *Artemia salina* NAUPLII

| ANIMAL NUMBER | A. GROUP 1 TIME: 1000–1740 | 1945–0015 | MEAN | B. GROUP 2 1020–1430 | 1545–2000 | 2000–2400* | 2400–0800* | 1220–1430 | 1530–1930 | MEAN |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1.04 | 1.85 | 1.45 | 1.68 | 2.67 | 1.60 | 0.63 | – | – | 1.64 |
| 2 | 1.47 | 1.91 | 1.69 | 0.96 | 0.82 | 3.47 | 1.57 | 1.20 | 1.71 | 1.54 |
| 3 | 2.21 | 2.27 | 2.24 | 0.74 | 0.54 | 1.87 | 2.57 | 1.68 | 1.22 | 1.44 |
| 4 | 2.16 | 1.59 | 1.87 | 0.91 | 0.84 | 2.13 | 1.71 | 1.44 | 0.98 | 1.57 |
| 5 | 2.12 | 2.04 | 2.08 | 0.23 | 2.00 | 2.40 | 2.14 | 2.64 | 2.68 | 2.10 |
| 6 | 1.80 | – | 1.80 | 2.27 | 2.50 | 1.91 | 1.86 | 1.92 | 2.44 | 2.15 |
| 7 | – | – | – | 2.66 | 0.25 | 1.36 | 1.43 | 0.96 | 2.20 | 1.63 |
| MEAN | 1.60 | 1.93 | 1.80 | 1.35 | 1.37 | 2.11 | 1.70 | 1.64 | 1.87 | 1.70 |

NOTE: Observations on two different groups of individually fed animals were made. Values in field of table are nauplii ingested per hour. The experiment for group 1 was run 23–24 March 1968; the experiment for group 2 was run 31 May-1 June 1968.

* Run in darkness.

TABLE 5

FEEDING RATES OF GROUPS OF *Lucifer chacei* ON *Artemia salina* NAUPLII

| EXPERIMENTS | NUMBER OF *Artemia* PER *Lucifer* PER HOUR WITHOUT PHYTOPLANKTON | WITH PHYTOPLANKTON | WITHOUT PHYTOPLANKTON |
|---|---|---|---|
| Experiment *A* | – | 0.886 | 0.565 |
| Experiment *B* | FIRST RUN | SECOND RUN | |
| Bowl 1 | 0.94 | 1.17 | – |
| Bowl 2 | 1.20 | – | 1.09 |
| Bowl 3 | 0.97 | 1.57 | – |
| Bowl 4 | 0.85 | – | 0.82 |
| Experiment *C* | STARVED ANIMALS | NORMAL ANIMALS | |
| Mean | 1.45 | 0.76 | |
| No. Determinations | 2 | 5 | |
| Standard Error | 0.56 | 0.94 | |

NOTE: Approximately 10 *Lucifer chacei* and approximately 160 *Artemia salina* were placed in bowls containing 1,400 ml of water. *A*, rates by two different groups – one with *Artemia* and phytoplankton as food, the other with just *Artemia* as food; *B*, rates by four different groups, the first run with all groups fed just *Artemia*, the second with phytoplankton also added to two bowls; *C*, rates by one starved group and one normal group of *Lucifer*.

TABLE 6

RESPIRATION OF COMBINED LARVAL AND ADULT STAGES OF *Lucifer chacei*

| STAGE | RESPIRATION PER ANIMAL: MEAN ($10^{-5}$ mg $O_2$/h) | NO. | STANDARD ERROR | $10^{-4}$ calories/h | $10^{-3}$ $\mu$g $O_2$/h per g ash-free organic | $\mu$liter $O_2$/mg wet wt/h |
|---|---|---|---|---|---|---|
| Adults | 13.6 | 13 | 1.42 | 4.59 | 1.0 | 198 |
| Schizopods | 3.3 | 3 | 0.58 | 1.12 | 3.0 | – |
| Protozoea-Zoea | 0.43 | 8 | 0.103 | 0.145 | 0.5 | – |

NOTE: Values were converted to cal/h by use of the oxy-calorific equivalent (Phillipson 1966).

TABLE 7

ASSIMILATION OF PHYTOPLANKTON AND ZOOPLANKTON BY *Lucifer chacei*

*A*. Assimilation of *Dunaliella tertiolecta*

| STAGE | CALORIES × $10^{-4}$/h: INGESTED | ASSIMILATED | % ASSIMILATION | NO. | STD ERROR (%) |
|---|---|---|---|---|---|
| Adults | 65.9 | 5.25 | 7.72 | 5 | 1.49 |
| Schizopods | 31.6 | 3.28 | 10.43 | 3 | 0.59 |
| Protozoea-Zoea | 10.9 | 1.10 | 10.10 | 4 | 1.67 |

*B*. Assimilation of *Artemia salina* by adult *Lucifer*

| EXPERIMENT NO. | MEAN ASSIMILATION RATIO (%) | NO. DETERMINATIONS | STD ERROR (%) | DURATION OF FEEDING (h) |
|---|---|---|---|---|
| 1 | 22.5 | 12 | 3.77 | 6–7 |
| 2 | 21.4 | 5 | 2.89 | 13–14 |

(1961) value of 6,700 calories per ash-free gram. The ash content of my *Artemia* was 23.1 percent of dry weight, giving 5,152 calories per gram of dry *Artemia*. The mean dry weight of the *Artemia* nauplii was 0.0022 mg.

The results of "micro-Winkler" determinations of oxygen used by *Lucifer* are shown in Table 6. Adult respiration was $1.36 \times 10^{-4}$ mg of oxygen/h. This converts to 198 $\mu$liter/mg wet weight per hour based on a wet weight of adult *Lucifer* of 0.96 mg. The value obtained for the respiration falls within the range of other zooplankton summarized by Wolvekamp and Waterman (1960). Mean schizopod respiration was $3.3 \times 10^{-5}$ mg $O_2$/h, and the combined protozoea-zoea stages respired $4.3 \times 10^{-6}$ mg $O_2$/h.

Respiration per gram organic dry weight was higher in schizopods than adults (Table 6), which agrees with the general observation that metabolism is higher per unit weight in smaller animals (Phillipson 1966). However, the zoea-protozoea stages appear to have the lowest respiration per gram dry weight.

Oxygen uptake was converted to calories by use of the "oxy-calorific" equivalent (Phillipson 1966). Each milligram of oxygen consumed represents the loss of 3.38 calories as heat. Thus, an adult *Lucifer* uses $4.59 \times 10^{-4}$ cal/h, schizopods use $1.1 \times 10^{-4}$ cal/h, and zoea-protozoea use $1.45 \times 10^{-5}$ cal/h.

Data from assimilation experiments are contained in Table 7. Assimilation of phytoplankton by all stages was between about 7 to 10 percent. Mean assimilation of animal food by adults was 22 percent. No differences in assimilation related to *Lucifer* body length, feeding period duration, or number of *Artemia* ingested were observed.

TABLE 8

GRAZING RATE OF PROTOZOEA-ZOEA STAGES OF *Lucifer chacei* ON *Dunaliella tertiolecta* AT DIFFERENT CELL CONCENTRATIONS

| (ALGAL CELLS/ml) × $10^3$ | | DURATION (h) | NO. | ($k$*/ANIMAL) | VOLUME SWEPT | CELLS INGESTED/ |
|---|---|---|---|---|---|---|
| START ($N_o$) | END ($N_t$) | ($t$) | ANIMALS | × $10^{-3}$ | CLEAR (ml/h) | ANIMAL PER HOUR |
| 57,000 | 26,200 | 13.3 | 62 | 0.94 | 0.28 | 1,046 |
| 30,400 | 10,500 | 10.5 | 65 | 1.6 | 0.48 | 898 |
| 26,500 | 5,600 | 10.5 | 81 | 1.8 | 0.55 | 737 |
| 26,500 | 7,700 | 10.3 | 66 | 1.8 | 0.53 | 802 |

$$*k = -\frac{lnN_t - lnN_o}{t}.$$

## DISCUSSION

Before the data may be used to construct an energy flow model for *Lucifer chacei*, a critical examination of the data and a comparison with results from other investigators are in order. The estimated calorific value per ash-free gram of adult *Lucifer* is consistent with observations on other zooplankton (Richman 1958, Golley 1961, and Slobodkin and Richman 1961). Calorific value per ash-free gram of larval stages of *Lucifer* is high when compared with the above observations. The ash content of the larval stages is also high when compared to other pelagic Crustacea (Vinogradov 1953, Raymont et al. 1964). Incomplete removal of salt may have interfered with my determinations.

Results of a feeding experiment where phytoplankton was used as food indicate that the protozoea stages may not have filtered water at a constant rate. Filtration of a constant volume of water regardless of cell concentration would have caused an exponential decrease in the algal population if no phytoplankton was added by cell division or lost by sinking. Under conditions of filtration of constant water volumes the instantaneous rate of decrease in the phytoplankton population caused by grazing should be constant and independent of cell concentration, although the grazing rate itself will vary with the concentration. The data contained in Table 8 indicate that the rate, $k$, varied with cell concentration. The volume of water "swept free" (Gauld 1951) also appeared to change with food concentration, as greater volumes were swept free in flasks with a lower initial density of phytoplankton. These values were tested statistically (Charles Miller, personal communication) and a significant difference was found between filtering rates at the high and low concentrations. These data, plus the observation that feeding decreased when dinoflagellates were present or increased with starvation, indicate selectivity in the species preferred and regulation of rate of feeding on phytoplankton; i.e., ingestion of phytoplankton may have been an active process rather than the result of passive filtration of a constant volume of water. Similar rejection of certain algal cultures by selectively feeding has been reported by Lasker (1966) and Conover (1964).

For these reasons phytoplankton ingestion rates were determined by considering them to be independent of cell concentration. The rates were calculated by dividing the number of cells removed by the number of animals added to the phytoplankton solution. All values were reduced to cells ingested per hour by dividing the above value by the duration of each experiment.

Weight per *Dunaliella* cell was $2.5 \times 10^{-10}$ g, a value very similar to the weight Richman (1958) determined per *Chlamydomonas* cell ($2.48 \times 10^{-10}$ g). If Richman's mean of 5,340 cal/g of Chlorophyceae is correct, then the mean number of calories per *Dunaliella* cell is $1.34 \times 10^{-6}$. These values were used to determine that adult *Lucifer* ingest energy in the form of *Dunaliella* at a rate of $6.59 \times 10^{-3}$ cal/h, combined schizopod stages ingest $3.16 \times 10^{-3}$ cal/h, and combined zoea-protozoea stages ingest $1.1 \times 10^{-3}$ cal/h.

Feeding rate on *Artemia* was greater for individually feeding adults than for adults feeding together in 8-inch bowls. Either container size or crowding may have had some effect.

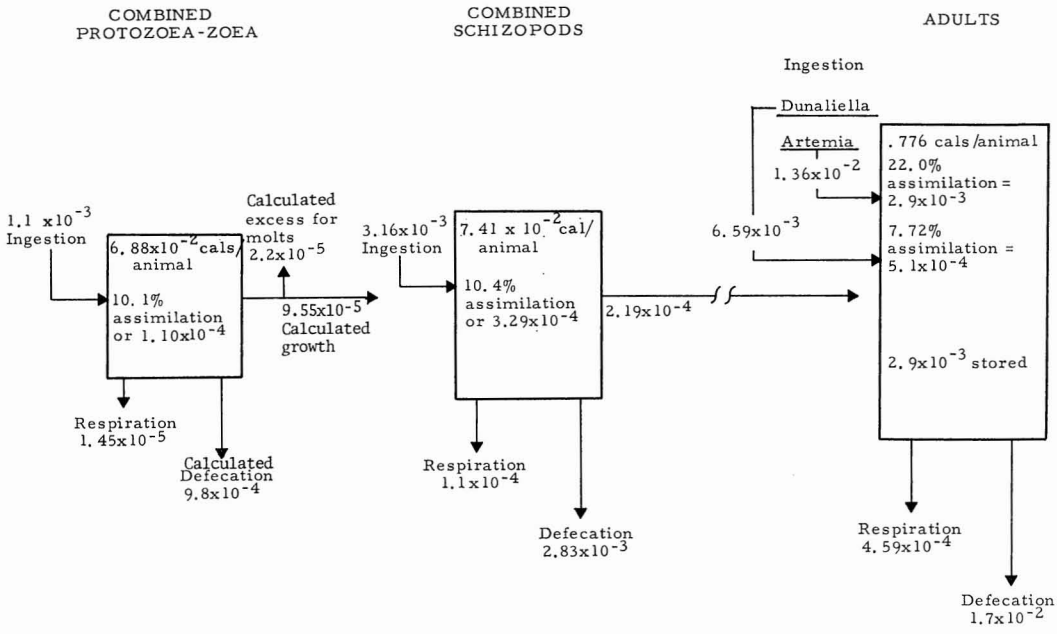


FIG. 2. Diagrammatic energy transformations by *Lucifer chacei* from early larval stages through adult. All values are calories per h/animal.

Often when numbers of *Lucifer* were present in a bowl, they occurred together in the area nearest the light. Perhaps the movement of other *Lucifer* in the same area inhibited feeding, or swept the *Artemia* away.

I do not know why the feeding rate increased when phytoplankton was given as food along with *Artemia*. Anraku and Omori (1963) have shown that omnivorous copepods have a reduced predation rate on animal food when phytoplankton is introduced. A voluminous literature has developed concerning the release of metabolites by primary producers (Lucas 1961). According to Hardy's and Gunther's (1935) "exclusion principle," these metabolites may have a negative effect on grazing. Perhaps some of these metabolites cause an increase in feeding under certain circumstances.

As was mentioned previously, respiration per gram organic body weight was lower in zoea and protozoea than in adult stages. This is in contrast with the generalization that respiration per gram body weight decreases with size (Phillipson 1966). No direct cause for the lower rate in the larvae was observed.

The assimilation values using $^{35}S$ were low relative to those of other workers (Welch 1968). It is probable that sulfur, although occupying a position similar to carbon in the periodic table, does not provide an adequate measure of the carbon balance of living systems. Sulfur is an important element in the amino acids methionine, cystine, and cysteine. These amino acids contribute the bulk of sulfur to the economy of animals (Forbes 1962). The ultimate fate of cystine in animals is the formation of inorganic sulfates which are rapidly excreted. Crustacea tend to excrete sulfate ions to maintain their ionic equilibrium (Robertson 1960). Sulfur may also be concentrated among the more undigestable tissues such as the *Artemia* exoskeleton (Sidney J. Townsley, personal communication); therefore, a greater percentage of sulfur than of carbon might be egested by *Lucifer* feeding on *Artemia*. These activities would tend to lower the apparent assimilation.

Another factor must be considered in a critical evaluation of the 22-percent assimilation efficiency. *Artemia* were given 15 hours to eliminate undigested radioactive phytoplankton from their guts, as Conover (1964) mentions that they are slow to egest their food when no

other particles are being ingested to keep the process moving. They were then fed to adult *Lucifer*, and assimilation was calculated with no further loss in radioactivity by *Artemia* being presumed. Controls indicated, however, that there was a reduction in the radioactivity of the *Artemia* during the period in which the first group of *Lucifer* was feeding on them. There was no information to indicate whether this difference was lost in an exponential or linear manner. Thus, because there was little difference in assimilation between animals fed for 6–7 hours or 13–14 hours, I have used the conservative 22-percent value in the energy model; although more information on how the *Artemia* lost their radioactivity would undoubtedly increase the apparent assimilation. If all of the difference in radioactivity had been lost initially (before *Lucifer* began feeding on *Artemia*), the assimilation would have been approximately 40 percent. This would be the upper limit.

An overall energy transformation diagram has been attempted from the results of this study (Fig. 2). It is assumed that feeding is continuous in this diagram. Such an assumption may be somewhat unrealistic as noted earlier, but the numbers used in computation were often derived from long-term experiments carried out during all periods of the night and day, and the hourly transfer rates probably represent mean rates.

The combined protozoea-zoea stages assimilate $1.1 \times 10^{-4}$ calories per hour; $1.45 \times 10^{-5}$ of the assimilated calories are lost per hour through respiration, leaving $9.55 \times 10^{-5}$ calories for growth. The calorific value of one animal is $6.88 \times 10^{-2}$ calories. Approximately 3 days later the animals' average size will equal a hypothetical "mid-schizopod" stage. In these 72 hours they will have accumulated $6.87 \times 10^{-3}$ calories, making their total calorific value prior to entering the next stage $7.57 \times 10^{-2}$. The calorific value of the combined schizopod stages is $7.41 \times 10^{-2}$. This indicates that the difference, $1.6 \times 10^{-3}$ calories or 2.3 percent of its total calorific value, may have been lost with the molts. This value is lower than Lasker's (1966) value of 4-percent energy loss with each *Euphausia pacifica* molt. It is possible that larval *Lucifer* may molt several times within a stage without showing measurable growth (Brooks 1882). This would further lower the estimated loss per molt.

The combined schizopods assimilate $3.3 \times 10^{-4}$ calories per hour and lose $1.1 \times 10^{-4}$ calories through respiration. The difference, $2.2 \times 10^{-4}$ calories per hour, is stored, presumably as growth. Approximately 17 days later, these animals will be adults with a calorific value of 0.776 calories per animal. Starting with $7.41 \times 10^{-2}$ calories per day and ingesting $3.3 \times 10^{-4}$ calories per hour for 17 days, an animal could not accumulate enough energy to equal 0.776 calories. Consequently there may be some change in the feeding habits or amount of phytoplankton food consumed by the animals between the schizopod and adult stage.

Animals kept in an aquarium for a few days were almost always found on or near the bottom in an oblique or vertical position. They appeared to be feeding on clumps of phytoplankton and their intestines were always highly colored due to the presence of large quantities of algae. They were able to molt and grow to the adult stages. In the pelagic realm, however, where such high concentrations of phytoplankton are rarely encountered, the animals may have to become omnivorous in order to store enough energy to grow normally. It is also possible, however, that due to the nature of the isotope and its form of metabolism that the assimilation values were too low relative to carbon assimilation. An assimilation of 59 percent of ingested phytoplankton, not an improbable value (Welch 1968), would allow them to reach an adult value of 0.776 calories per animal in 17 days if there were no energy losses other than from respiration.

The adults are able to assimilate a large quantity of energy in the laboratory. The number of calories ingested was computed by combining the average predation rate of *Lucifer* on *Artemia* in the 8-inch bowls containing both *Artemia* and phytoplankton with the average ingestion rate of *Dunaliella* by adult *Lucifer*. These values should most nearly simulate the situation in Kaneohe Bay where there is a mixed phytoplankton-zooplankton community. The value obtained was $3.4 \times 10^{-3}$ cal/h. This laboratory value may be high because zooplankton of the size and abundance of the *Artemia* fed to

TABLE 9

GROSS AND NET GROWTH EFFICIENCIES OF *Lucifer chacei*

| EFFICIENCIES | ZOEA-PROTOZOEA | SCHIZOPODS | ADULTS | COMBINED MEAN |
|---|---|---|---|---|
| Gross Growth Efficiency | 9.2 | 6.9 | 14.4 | 10.2 |
| Net Growth Efficiency | 90.9 | 66.7 | 85.7 | 81.1 |

NOTE: Adult values were calculated using combined ingestion of *Dunaliella tertiolecta* and *Artemia salina*.

*Lucifer* may not be available. Also, the calorific value of *Artemia* nauplii may be higher than *Lucifer*'s natural food (Slobodkin and Richman 1961).

Only $4.59 \times 10^{-4}$ calories are lost through respiration, a rate which allows the storage of $2.84 \times 10^{-3}$ calories per hour. At this rate it would only take approximately 11 days for an adult *Lucifer* to double its calorific value, which is less than half the time necessary for the other stages. This excess might be incorporated into reproductive products and molts.

Gross and net growth efficiencies (Conover 1964) were calculated for all stages of *Lucifer chacei* (Table 9). When data for all stages were combined, the mean gross growth efficiency was 10.15 percent, and the mean net growth efficiency was 81.10 percent. These values compare well with values in the literature (Conover 1964, Welch 1968). Gross growth efficiency may be used to estimate the upper limit of ecological efficiency (Slobodkin 1961) if it is assumed that all *Lucifer chacei* will be consumed by a predator. The often quoted value of 10 percent for ecological efficiency would be an upper limit for *L. chacei* in this study.

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